NALS OF THE SOUTH AFRICAN MUSEUM

NALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 56 Band
September 1970 September
Part 4 Deel

THE PALATE AND MANDIBLE IN SOME SPECIMENS OF *DICYNODON TESTUDIROSTRIS* BROOM & HAUGHTON (REPTILIA, THERAPSIDA)

By

M. A. CLUVER

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad

OUT OF PRINT/UIT DRUK

1, 2(1, 3, 5, 7–8), 3(1–2, 5, t.–p.i.), 5(2, 5, 7–9), 6(1, t.–p.i.), 7(1–3), 8, 9(1–2), 10(1), 11(1–2, 5, 7, t.–p.i.), 21, 24(2), 27, 31(1–3), 33, 38, 44(4).

Price of this part/Prys van hierdie deel

R2.60

Printed in South Africa by
The Rustica Press, Pty., Ltd.
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.
Courtweg, Wynberg, Kaap

THE PALATE AND MANDIBLE IN SOME SPECIMENS OF *DICYNODON TESTUDIROSTRIS* BROOM & HAUGHTON (REPTILIA, THERAPSIDA)

By

M. A. Cluver

South African Museum, Cape Town

(With 12 figures)

[*MS. accepted* 30 *July* 1970]

Contents

	PAGE
Introduction	133
Some features in the cranial anatomy of *Dicynodon testudirostris*	134
Extent of the horny beak in *Dicynodon testudirostris*	140
Jaw musculature and masticatory cycle in *Dicynodon testudirostris*	140
Comparison with other forms	144
Discussion	150
Summary	152
Acknowledgements	152
References	152
Abbreviations	153

Introduction

During the course of a study on the functional anatomy of the mandible and palate in the advanced dicynodont genus *Lystrosaurus* (Cluver, in press) several *Cistecephalus* and *Endothiodon* zone dicynodont specimens were examined and freed of matrix. It became apparent that both mandible and palate in these specimens were subject to considerable structural variation, and that the variations could be of functional significance in that they were probably associated with differences in the masticatory cycle.

Crompton & Hotton (1967) have given a comprehensive account of the different stages in the masticatory cycle of the dicynodonts *Emydops* and *Lystrosaurus*, and pointed out the main differences between the two genera in this respect. Important points in Crompton & Hotton's work are the following:

(i) the temporalis and pterygoideus musculature in dicynodonts would have permitted a retractive power stroke only during mastication,

(ii) in an endothiodontid such as *Emydops* use was made of an anterior 'beak bite' between the upper and lower jaws, distinct from a cutting action between the upper and lower teeth and the expanded palatal portion of the palatine.

(iii) *Lystrosaurus*, on the other hand, utilized a slicing action between the lower beak and the close-fitting palatal rim in front of the tusks.

These authors state that crushing did not take place in the *Lystrosaurus*

Ann. S. Afr. Mus. **56** (4), 1970: 133–153, 12 figs.

masticatory cycle, which was adapted solely for slicing action. However, examination of several well-preserved and undistorted skulls and lower jaws of *Lystrosaurus* (Cluver, in press) has shown that crushing between the lower jaw and the expanded palatal portion of the palatines took place at the end of the retractive stroke, where the dorsal surface of the dentary closely approaches the palatal roof.

Important in the reconstruction of this mechanism are the probable areas of insertion of the jaw adductor muscles. Crompton & Hotton (1967) based their calculations on the strong likelihood of the external adductor muscles having inserted on a lateral dentary shelf and in a deep sulcus on the dorsal edge of the dentary. These features appeared to be common among the majority of dicynodonts.

It is therefore of considerable interest that several dicynodontid specimens in the South African Museum collection differ from such diverse genera as *Emydops*, *Pristerodon*, *Dicynodon* and *Lystrosaurus* in the absence of both a dorsal dentary sulcus and a lateral dentary shelf. Correlated with this was the extremely unusual nature of the palate in these forms, which were identified as specimens of *Dicynodon testudirostris* Broom & Haughton, all, including the type specimen, from the *Cistecephalus* zone of the Beaufort Series.

The new features uncovered during the preparation of the palate of the type specimen of *Dicynodon testudirostris*, and the unusual structure of the palatal rim and mandible in the referred specimens, warrant an additional description of the species, which in several important respects differs sharply from other species of *Dicynodon*.

In the following, the term *dicynodont* has reference to members of the infraorder Dicynodontia (*sensu* Romer, 1966), while the terms *dicynodontid*, *endothiodontid* and *lystrosaurid* refer respectively to members of the families Dicynodontidae, Endothiodontidae and Lystrosauridae.

Some features in the cranial anatomy of *Dicynodon testudirostris*

1. Type specimen, S.A.M. Cat. No. 2354 (Fig. 1).

Locality: Dunedin, Beaufort West.

The type skull has been described and illustrated by Broom & Haughton (1913) and Broom (1932). On the skull roof (Fig. 1b) the intertemporal region is narrow and the postorbitals meet over the parietals. The preparietal is broad anteriorly but narrows posteriorly to form only a small part of the border of the pineal foramen. There is a fairly long, very narrow postfrontal. The maxilla extends far upwards on the side of the snout to meet the nasal, and separates the short lacrimal from the septomaxilla. The prefrontal has only a limited extent on the skull roof.

The hitherto undescribed palate (Fig. 1c) of the type skull was completely cleared of matrix and several unusual features were uncovered. Although there

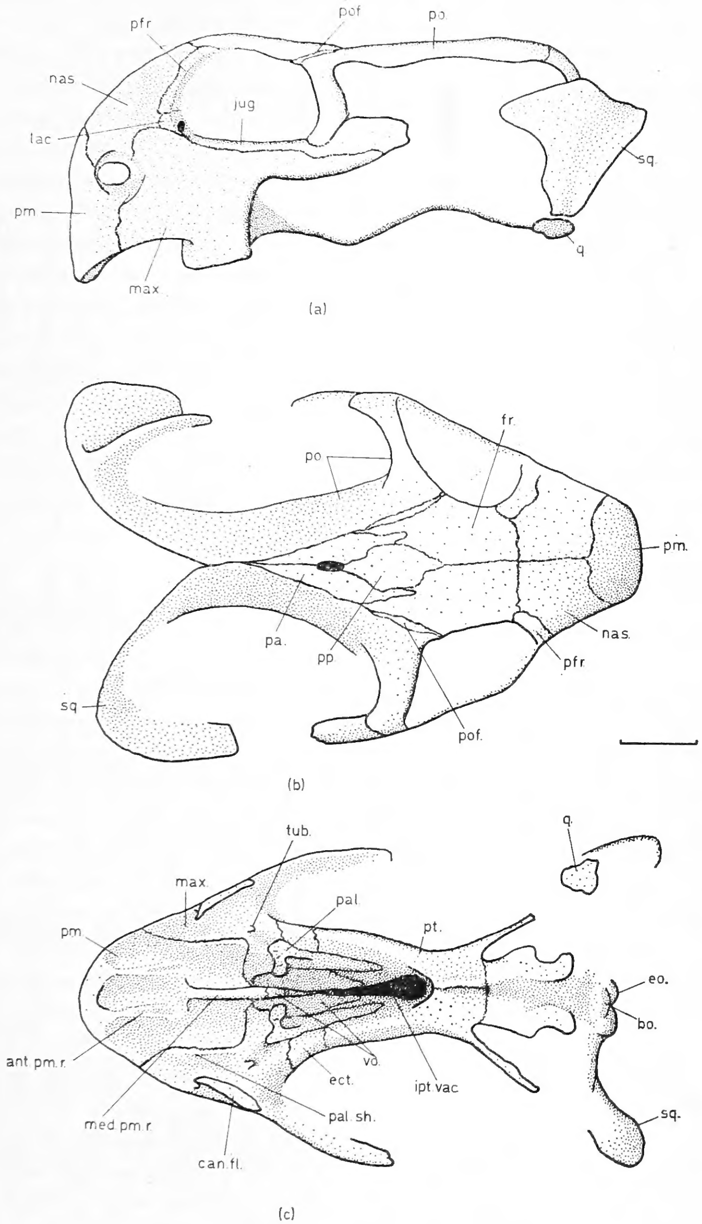

FIG. 1. Skull of *Dicynodon testudirostris*. Type specimen, S.A.M. Cat. No. 2354. (a) lateral (b) dorsal (c) ventral view. × 1. Scale = 1 cm.

is no indication of a canine tusk, the relationships between palatine, premaxilla and maxilla place the species in the genus *Dicynodon* as defined by Toerien (1953). The palatine has a small palatal surface and does not reach the premaxilla anteriorly. The maxilla therefore forms the lateral border of the anterior palatal notch.

The palatal surface of the premaxilla bears a pair of anterior palatal ridges, as is found in many dicynodonts, as well as the typical median ridge which extends back to meet the vomer.

The maxilla is produced ventrally as an enlarged caniniform process, which is incomplete on both sides of the specimen (Fig. 1c, can. fl.). Initially broad-based, this flange tapers rapidly to form a blade which was obviously continued further ventrally during life. The preserved portion of the blade is rounded posteriorly but carries a sharp anterior cutting edge. This sharp edge of the flange is carried medially to the equally sharp palatal rim, and between the two edges a recess is formed. In ventral view it can be seen that the maxillary flange is turned quite sharply inwards.

In contrast to dicynodonts in which the roof of the palate is smoothly and evenly excavated, the premaxilla and maxilla in this species are built up medially to the maxillary flange to form a raised shelf (Fig. 1c, pal. sh.), equal in height to the median premaxillary ridge. A deep trench is thus formed between the lateral shelf and the median ridge.

Anterior to the caniniform flanges the palate is broad and bounded laterally by a shallow palatal rim. Anteriorly the rim, formed by the premaxilla, is deeper and terminates as two laterally placed processes, continuations of the anterior palatal ridges. Between them the two processes separate a shallow median cleft.

The reduced palatal surface of the palatine lies slightly recessed above the level of the raised anterior maxillary and premaxillary shelf. A thin median process of the palatal portion of the palatine extends in towards the median vomerine septum, tending to separate off the anterior palatal notch of the internal nares.

At the posterior limit of the raised premaxillary-maxillary shelf, and medially to the posterior limit of the maxillary caniniform flange, the maxilla is drawn out into a rounded, pointed tubercle (Fig. 1c, tub.).

2. Referred specimen, S.A.M. Cat. No. 10086 (Figs 2, 3).

Locality: Dunedin, Beaufort West.

This specimen is an almost complete skull and mandible, only part of the right zygomatic arch being missing. The skull is only slightly dorso-ventrally compressed. It was possible to remove the mandible entirely without damage to the specimen, and the relationships between palate and mandible could be accurately determined.

Basically, the skull differs from that of the type specimen only in its

completeness and slightly larger size. On the skull roof the postorbitals meet over the parietals, the preparietal is inflated anteriorly, the postfrontal is a narrow strip of bone, and the prefrontal has a limited extent on the outer skull roof. The maxilla rises up high behind the nostril to separate the lacrimal from the septomaxilla.

The palate is identical to that of the type specimen, but the caniniform flanges of both sides are preserved in their entirety. It can now be seen that each flange terminates ventrally as a sharp, curved edge (Fig. 2).

In the mandible (Fig. 3) the post-dentary bones, which appear to be of the normal dicynodont pattern, have undergone a slight downward shift in relation to the dentary, which has several unusual characteristics. There is no

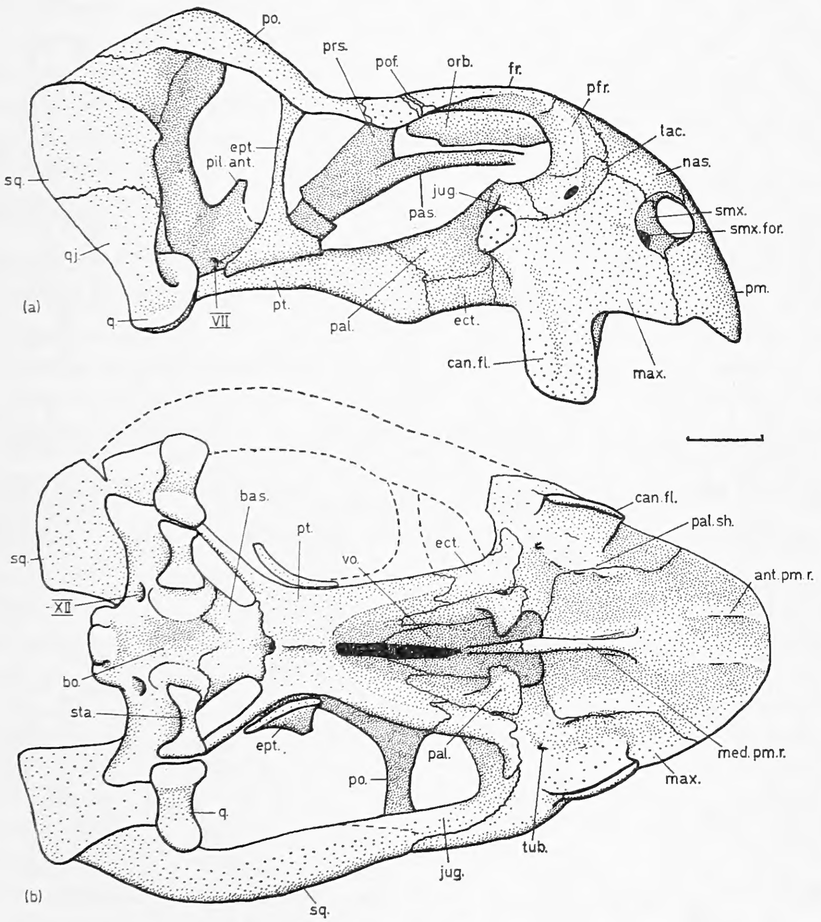

FIG. 2. Skull of *Dicynodon testudirostris*. S.A.M. Cat. No. 10086. (a) lateral (b) ventral view. × 1. Scale = 1 cm.

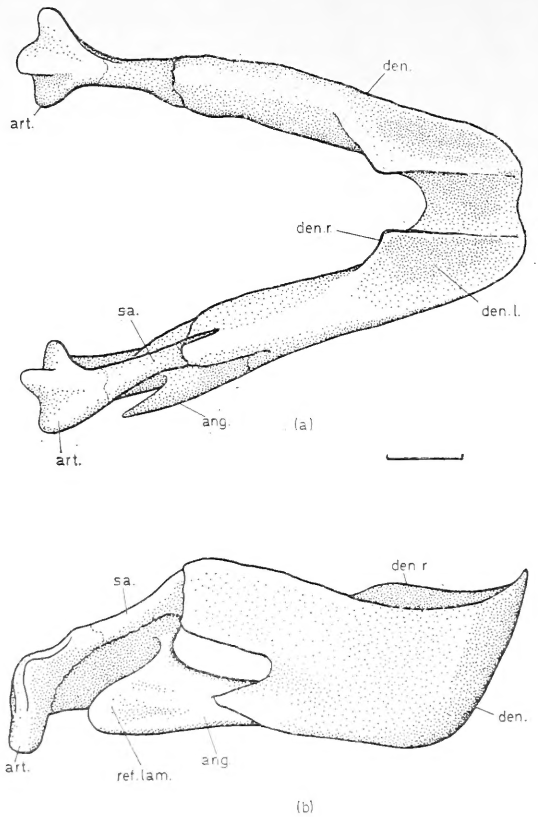

FIG. 3. Mandible of *Dicynodon testudirostris*. S.A.M. Cat. No. 10086. (a) dorsal (b) lateral view. × 1. Scale = 1 cm.

lateral dentary shelf such as is found in *Emydops*, *Pristerodon*, *Lystrosaurus*, *Daptocephalus* and *Kingoria*, and which is supposed to have provided an effective insertion area for the lateral division of the external adductor muscle mass. Similarly, the dorsal edge of the dentary is smoothly rounded, and shows no trace of the deeply incised trench found in other dicynodonts, which is thought by some authors to have provided attachment for an inner division of the external adductor muscle mass. In the symphyseal region the dentary is not as deep as in the mandible of other edentulous dicynodonts. Medially the dorsal surface of each dentary is built up on either side of a deep median trough as a pair of sharp-edged longitudinal ridges (Fig. 3, den. r.). Each ridge terminates as a sharp process on the anterior surface of the mandible, and is produced backwards past the main body of the jaw ramus. These ridges lie in true parasagittal planes, and separate the deep median trough from two lateral, dorsally excavated, dentary ledges (Fig. 3, den. l.)

3. Referred specimen S.A.M. Cat. No. 10078 (Fig. 4).

Locality: Dunedin, Beaufort West.

This is a slightly distorted skull with mandible, lacking part of the occiput and right zygomatic arch, and the posterior part of the right jaw ramus.

The relationships of the bones of the skull roof are as in the type specimen, and a pair of caniniform flanges is present. The palate is identical to that of the previous two specimens, but preparation has revealed the presence of a small, partially erupted tooth lying flat against the medial surface of each caniniform flange. The teeth are in the position of the large canine tusks common in dicynodonts, but each tooth is contained in a recess in the caniniform flange, suggesting that it lay under the horny beak and was not functional.

In the North American dicynodont genus *Placerias*, Camp & Welles (1956) have described 'male' specimens with enlarged caniniform processes which almost completely enclose a non-functional tooth. In these skulls, however, the tooth is directed into the buccal cavity, and the tip has been worn down by the action of the dentary during mastication.

The mandible of this specimen was removed and cleared of matrix. In all respects it is identical to the mandible of specimen no. 10086.

4. Referred specimen S.A.M. Cat. No. 10377.

Locality: Noblesfontein, Victoria West.

This specimen is a skull lacking both zygomatic arches and the inter-temporal part of the skull roof. While the caniniform processes themselves have been sheared off close to the base on both sides, the characteristic notch between the base of the medial, anterior edge of the caniniform flange and the lateral

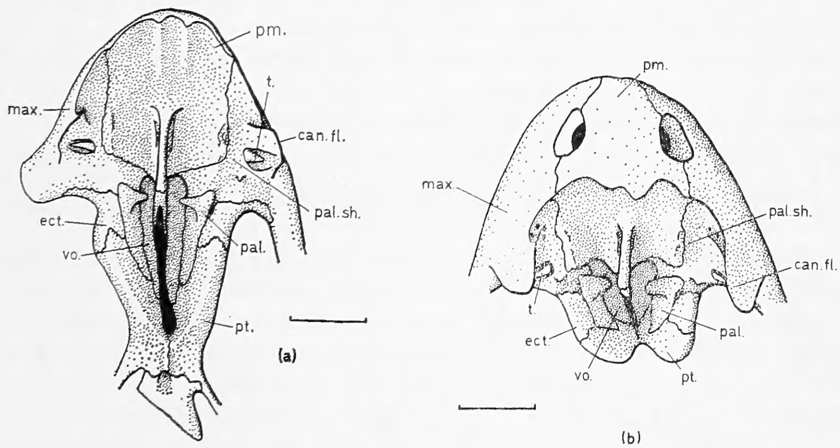

Fig. 4. Skull of *Dicynodon testudirostris*. S.A.M. Cat. No. 10078. (a) palatal (b) anteroventral view. × 1. Scale = 1 cm.

palatal rim is preserved on both sides. On the right side the section through the process has revealed a broken-off tooth in the same position, and of the same size, as the teeth in specimen no. 10078.

In addition to these described specimens, a superficial survey of the South African Museum dicynodont collection showed that additional specimens of *D. testudirostris* appear to be widespread in several *Cistecephalus* zone localities. Specimens showing the characteristic caniniform flange, mandible and skull roof of *D. testudirostris* have been collected at Kuilspoort, Beaufort West (e.g. S.A.M. 6550, 7401), Roosplaats, Beaufort West (e.g. S.A.M. 10204), Leeukloof, Beaufort West (e.g. S.A.M. 11084) and Loskop, Victoria West (e.g. S.A.M. 10060).

Extent of the Horny Beak in *Dicynodon testudirostris*

Several inferences can be made regarding the extent of the horny beak in the above specimens. The lateral palatal rim, which tapers to a sharp knife-edge, was apparently covered by a correspondingly sharp and probably thin layer of horn, produced anteriorly as two spiky processes over the bony projections of the premaxilla. To the rear the horny layer would have covered the caniniform flanges, extending as a sharp leading edge anteriorly. Several sizeable nutrient foramina in the notch between the leading edge and the lateral palatal rim suggest that a thickening of horn lay in this recess. Medially to the caniniform flange the presence of a horny pad is again indicated by nutrient foramina on the raised area of premaxilla and maxilla. The horn cover very likely extended beneath the roof of the secondary palate to form a cutting edge over the median palatal ridge.

A posterior extension of the beak appears to have capped the expanded palatal portion of the palatine.

On the mandible the beak appears to have terminated in a pair of sharp points similar to those of the upper jaw. Behind these spikes the horny layer must have continued as a pair of cutting edges, while laterally to each edge the lateral dentary depression would have contained a thicker horny pad. This pad probably terminated laterally as a clearly defined edge on the side of the mandible. The median trough between the two cutting edges was very likely also covered with at least a thin layer of horn.

Jaw Musculature and Masticatory Cycle in *Dicynodon testudirostris*

The rounded dorsal edge and flat lateral surface of the dentary in *Dicynodon testudirostris* suggest that the jaw adductor musculature was not inserted onto the mandible in the same way as in, for instance, *Emydops* or *Daptocephalus*. However, since the anatomy of the articular and quadrate in *Dicynodon testudirostris* has remained typically dicynodont and indicates the usual anteroposterior sliding action between the two bones, and since the areas of origin of the external adductor musculature on the rear of the skull have remained unchanged, it is safe to assume that the masticatory cycle was close to the usual dicynodont

pattern and that the external adductor muscles inserted on approximately the same portions of the dentary as in other dicynodonts. Thus the lateral division of the external adductor muscle probably arose from the quadratojugal and lateral parts of the squamosal and inserted over the lateral surface of the dentary, in the position of the dentary shelf in other dicynodonts. The medial division of the external adductor muscle would have had its origin inside the temporal fossa on the squamosal, parietal and postorbital, and probably inserted partly on the dorsal edge and partly on the inner or outer surface of the dentary, in the position of the dentary groove of other dicynodonts.

The main internal adductor muscles, i.e. the anterior and posterior pterygoideus muscles, probably had the same relationships as those reconstructed in *Emydops* by Crompton & Hotton (1967). The pterygoideus anterior muscle arose from the palatal ramus of the pterygoid and the lateral surface of the ectopterygoid, and wrapped around the lower edge of the articular and prearticular to insert on the outside surface of the prearticular beneath the reflected lamina.

The posterior pterygoideus muscle arose from its side of the characteristically moulded ventral surface of the interpterygoidal plate, and inserted beneath the internal condyle of the articular.

A depressor mandibulae muscle, now accepted as having been present in dicynodonts (Barry, 1967; Crompton & Hotton, 1967), would have originated on the occipital flange of the squamosal, and inserted on the ventrally directed retro-articular process of the articular.

Given these areas of origin and insertion, the jaw musculature would have been capable of the typical dicynodont masticatory cycle proposed by Crompton & Hotton (1967). However, the singular nature of the palate and anterior portions of the dentaries, results in occlusal relationships between upper and lower jaws which represent a departure from the condition in, for instance, *Daptocephalus* or *Lystrosaurus*.

1. Jaw from protracted, fully depressed position to protracted adducted position (Fig. 5a, b, c).

When the jaw is drawn up from the fully protracted position the sides of the dentary are able to move only a short way up past the caniniform flanges before the dorsal edge of the dentary touches the ectopterygoid (Fig. 5b, c). With the jaw slightly retracted before adduction, the overlap between caniniform flange and the dentary is increased, but actual contact between the flange and lateral dentary surface would be possible only if a considerable layer of horn were present on the dentary, and then the contact would be limited to one between the dentary and the inwardly directed leading edge of the flange. Lateral displacement of the mandible during mastication was probably possible during life, but the nature of the quadrate-articular contact in *Dicynodon testudirostris* seems to have kept such movement down to a minimum.

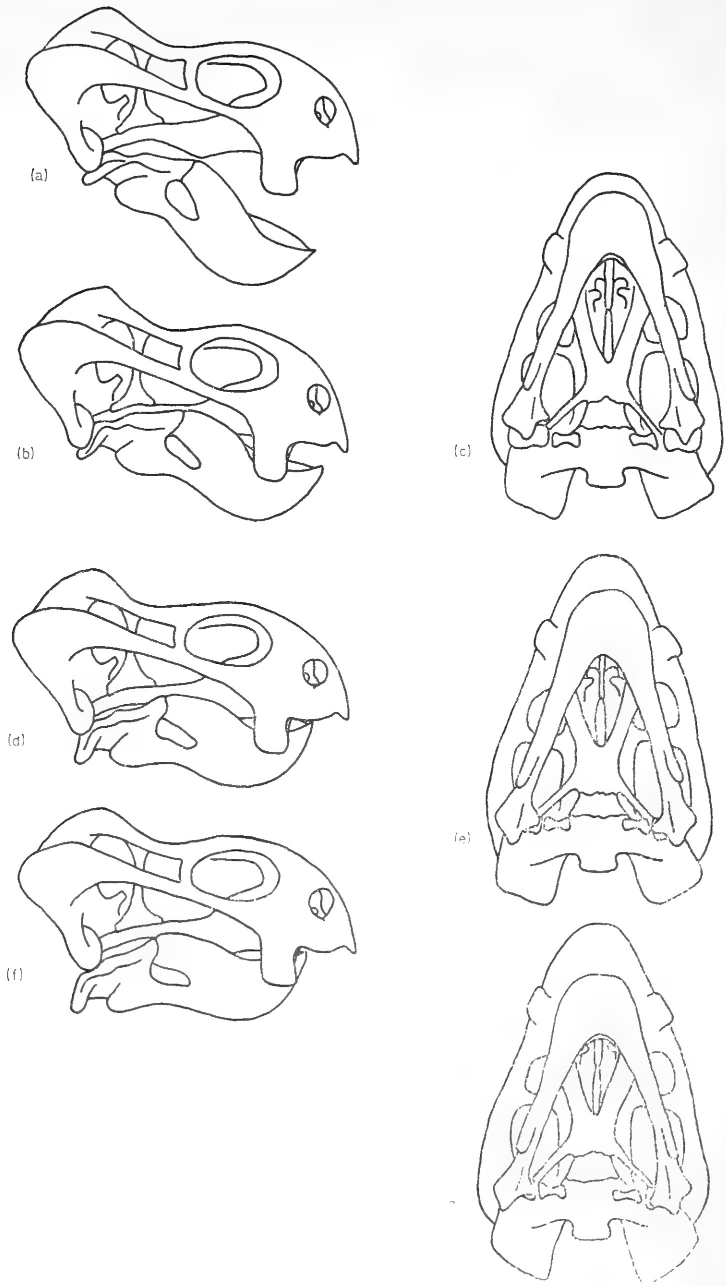

FIG. 5. Masticatory cycle of *Dicynodon testudirostris*. Lateral (a, b, d, f) and ventral (c, e, g) views.

2. Jaw fully protracted, fully adducted (Fig. 5b, c).

The anterior tips of mandible and premaxilla approach, but would have to be considerably produced as horn to make contact. The lateral palatal and mandibular rims are well separated, laterally as well as dorsoventrally, while the lateral dentary surface approaches the maxillary flange. The side of the mouth is still well open.

3. Jaw after beginning of retraction (Fig. 5d, e).

The dorsal, buccal surface of the fused dentaries moves up towards the palate, tending to close the side of the mouth in front of the caniniform flanges. However, the palatal and mandibular rims are still well separated laterally. The lateral dentary surface has passed the caniniform flange and the lateral excavation on the buccal surface of the dentary approaches the built-up area of the palate median to the flange.

4. Jaw fully retracted (Fig. 5f, g).

The anterior tip of the jaw lies in line with the front edges of the caniniform flanges, while the lateral dentary troughs appose the raised premaxilla-maxilla region. The median premaxillary palatal blade lies inside the median trench of the dentary symphyseal region.

Nowhere in the cycle does the lateral palatal rim, in front of the maxillary caniniform flanges, perform any prominent function. With the jaw in the adducted protracted position the anterior tips of the dentary and premaxilla approach each other, and the maxillary caniniform flanges overlap the lateral dentary surface, but the lateral palatal rim is well separated from the lateral dentary surface, both in ventral and in lateral view. As retraction proceeds, the anterior tip of the jaw moves upward, closing the gap in lateral view, but in ventral view it can be seen that the rounded dentary moves away from the lateral rim.

The caniniform flanges appear to have been functional mainly during the adduction of the lower jaw, and during the very first stages of retraction. After a short period of retraction the flat, lateral surface of the dentary has moved past the anterior cutting edge of the flange, which thereafter lies well separated from the rounded anterior portion of the dentary. A modest pad of horn on the side of the dentary, behind the rounded tip, would have been sufficient to give a working surface for the presumably sharp-edged, thin layer of horn on the caniniform flange.

During retraction, the lateral excavated area on the dorsal surface of the dentary approaches and apposes the built-up area of the maxilla and premaxilla, median to the maxillary caniniform flange. At the rear of each of the built-up areas is a short bony tubercle which projects towards the trough of the dentary table of its side, while the inner edge of each raised area bears less prominent tubercles. The horn pad housed in each dentary trough would have worked up against the horn-covered surface of the palate in a grinding, crushing action. The bony tubercles on the maxilla, if they were reflected in the covering horn

layer, would have assisted in stabilizing food during this crushing process.

At the end of retraction, the lateral dentary troughs move further upward, opposite the inflated palatal portions of the palatines.

During retraction, the pair of longitudinal cutting edges on the dorsal, buccal surface of the fused dentaries, which were covered by a correspondingly sharp layer of horn, project up into the trench between the raised lateral portion of the palate and the median premaxillary palatal ridge. These three sharp blades would have produced between them an effective slicing action. The terminal dentary spikes do not take an extensive part in this action, and approach the palatal trenches only at the end of retraction.

Comparison with Other Forms

Endothiodontidae

Emydops sp. S.A.M. Cat. No. 10153 (Fig. 6).

Locality: Dunedin, Beaufort West.

This is a well-preserved, undistorted skull. Canine tusks are absent, but there appear to be 4 postcanine teeth in both upper and lower jaw. In a number of teeth posterior serrations are visible. The palatal portion of the palatine is large and appears to make contact with the premaxilla. According to Toerien (1953) a palatine-premaxilla contact is characteristic of *Emydops.*

The palatal rim is well developed and sharp-edged, but it appears to become blunter posteriorly. There is a prominent median premaxillary ridge, but no indication of anterior premaxillary ridges. There is no clearly defined caniniform process.

The symphyseal region of the jaw is short, and the anterior tip of the

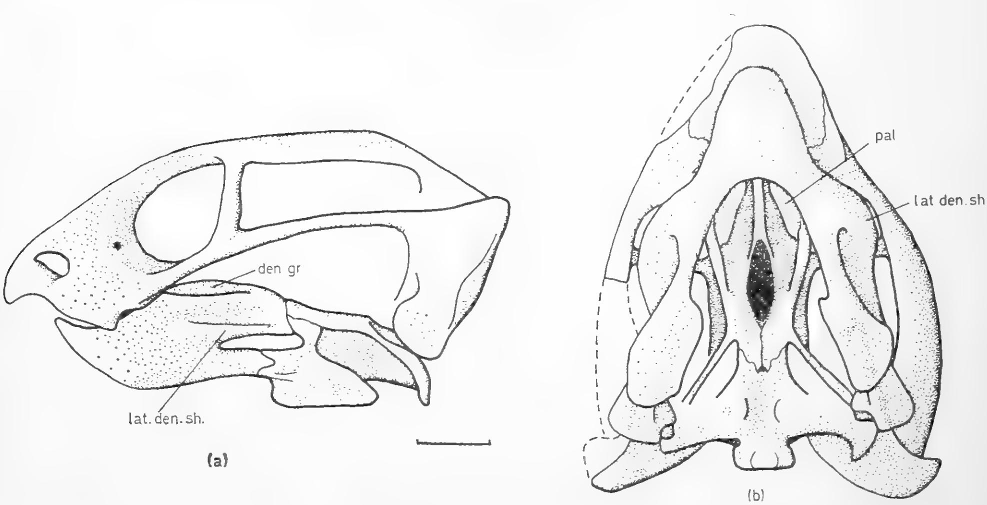

Fig. 6. Skull of *Emydops* sp. S.A.M. Cat. No. 10153. (a) lateral (b) ventral view. × 1. Scale = 1 cm.

dentary is produced dorsally as a blunt process. Immediately behind the symphyseal region the dorsal edge of the dentary is rounded, but further back there is a deeply incised trench lateral to the tooth row. The lateral surface of the dentary is drawn out to form a wide ledge above the mandibular fenestra.

Pristerodon (Information taken from Barry, 1967).

Canine tusks are present, as well as three postcanine teeth. The palatal rim is well developed anterior to the canine tusk. The palatine is not as large as in *Emydops*, and does not meet the premaxilla. Toerien (1953) has found this to be the case in the *Pristerodon* species he investigated. Anterior premaxillary ridges are not prominent.

Two functional teeth are present in each jaw ramus. As in *Emydops*, the symphyseal region is not extensive, and is produced to form a blunt anterior process. Both the dorsal dentary groove and the lateral dentary shelf are present.

Endothiodontid (?) sp. S.A.M. Cat. No. 10137 (Fig. 7).

Locality: Dunedin, Beaufort West.

Although tuskless and lacking postcanine teeth, this specimen resembles *Emydops* in size, the broad intertemporal region and palatine-premaxillary contact.

There is a median palatal ridge but no prominent anterior ridges. There is a weak caniniform thickening. The palatal surface of the palatine is large and meets the premaxilla anteriorly.

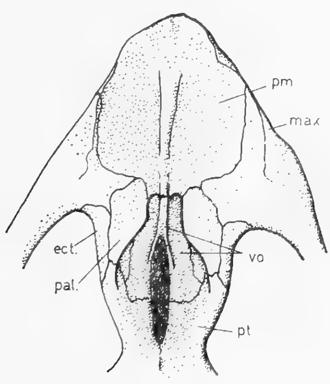

FIG. 7. Skull of endothiodontid (?) sp. S.A.M. Cat. No. 10137. Palatal view. × 1. Scale = 1 cm.

Cryptodontidae (*sensu* Toerien, 1953; Haughton & Brink, 1956)

Oudenodon kolbei, type specimen, S.A.M. Cat. No. 1886 (Fig. 8).

Locality: Rhenosterfontein, Beaufort West.

The palatal rim is drawn out as a modest caniniform process, a ventral continuation of a pronounced lateral thickening of the side of the snout. The

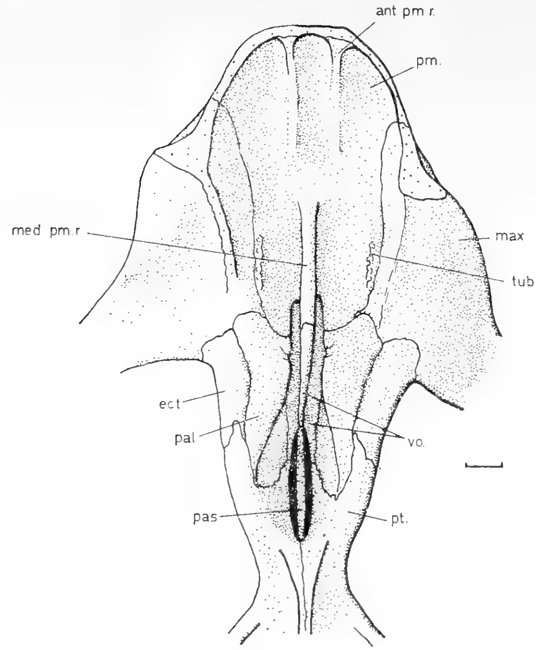

FIG. 8. Skull of *Oudenodon kolbei*. Type specimen, S.A.M. Cat. No. 1886. Palatal view. × ½. Scale = 1 cm.

palatal rim is well developed before and behind the caniniform process. All three premaxillary palatal ridges are present and prominent. Behind the level of the caniniform process the premaxilla is raised to form a ledge along the suture with the maxilla. The ledge is furnished with several sharp bony tubercles. The palatines are greatly expanded and make contact with the premaxilla.

Tuskless dicynodont, S.A.M. Cat. No. 10661 (Fig. 9).

Locality: Welgevonden, Fraserburg.

The mandible of this specimen has muscle scars on the lateral face of the dentary, which is not expanded to form a ledge. Behind the symphysis the dentaries are built up to form dentary tables (Fig. 9a, den. l.) (Crompton & Hotton, 1967). A deep dentary groove is present on the dorsal edge of the jaw ramus, and is continued forward as a shallow trough onto the dentary table or ledge. It seems probable that a pad of horn, carried in this anterior trough, would have acted against the palatine and adjoining premaxillary-maxillary portion of the palate during retraction of the jaw.

Dicynodontidae

Dicynodon grimbeeki (Information taken from Agnew, 1959).

The palatal rim is well developed in front of the tusks and the palatine does not reach the premaxilla.

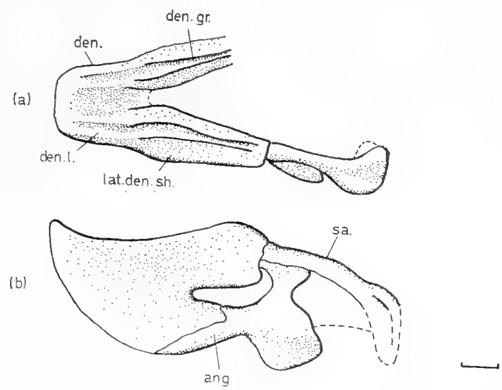

FIG. 9. Mandible of tuskless dicynodont sp. S.A.M. Cat. No. 10661. (a) dorsal (b) lateral view. $\times \frac{1}{2}$. Scale = 1 cm.

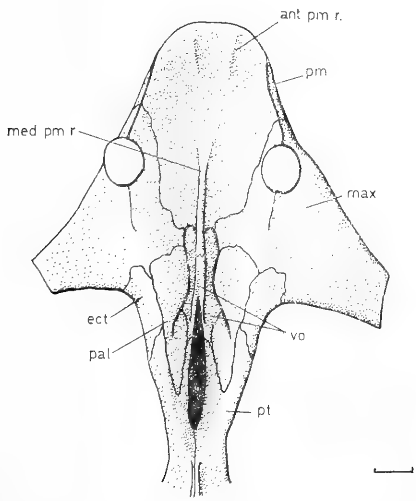

FIG. 10. Skull of *Dicynodon* sp. S.A.M. Cat. No. 10681. Palatal view. $\times \frac{1}{2}$. Scale = 1 cm.

Dicynodon sp. S.A.M. Cat No. 10681 (Fig. 10).

Locality: Leeukloof, Beaufort West.

The palatal surface is deeply recessed, and the palatal rim is strongly developed in front of the tusk and also to a lesser degree behind the tusk. The palatine does not reach the premaxilla. Anterior palatal ridges, as well as the posterior ridge, are present.

The jaw in several *Dicynodon* specimens possesses a dorsal dentary groove and built-up dentary tables, but no prominent lateral dentary ledge is found. Muscle scars in the region above the mandibular fenestra are present in some cases.

Daptocephalus sp. S.A.M. Cat. No. 8784.

Locality: Doornplaats, Graaff-Reinet.

Tusks are present and the palatal rim is strongly developed. Anterior palatal ridges as well as the posterior one are present. Ewer (1961) has described bony palatal tubercles on the palatine and adjoining maxilla. The palatine makes a short contact with the premaxilla.

The anterior part of each jaw ramus is built up to form dorsally grooved dentary tables, and a posterior dorsal dentary sulcus is present. The lateral surface of the dentary is moulded to form a weak ledge, and muscle scars are visible in this region.

Lystrosauridae (Fig. 11)

Several well-preserved skulls with mandibles were available for comparison. The palate is deeply recessed and bears clear anterior and posterior palatal ridges, while the surface of the maxilla alongside the palatal portion of the palatine is rough and pitted. In the lower jaw dentary tables and a dentary groove are present, and a clear dentary shelf is formed, although the latter is not as pronounced as in, for instance, the mandible of *Emydops*.

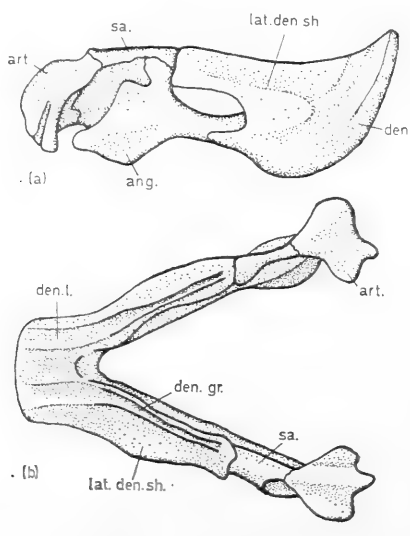

Fig. 11. Mandible of *Lystrosaurus*. Nat. Mus. Bloemfontein Cat. No. C. 403. (a) lateral (b) dorsal view. × ½. Scale = 1 cm.

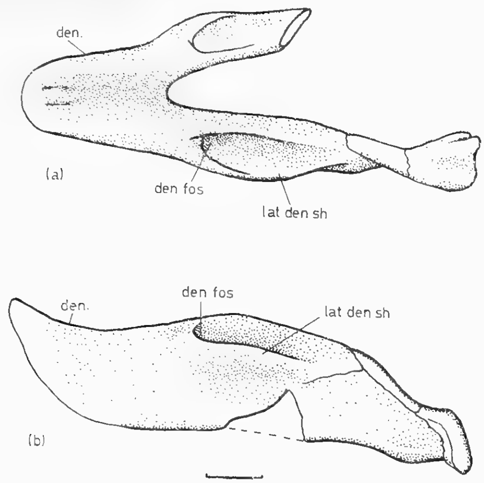

FIG. 12. Mandible of *Kingoria* (?). S.A.M. Cat. No. 6043. (a) dorsal (b) lateral view. × ¾. Scale = 1 cm.

Dicynodont (*Kingoria?*)

S.A.M. Cat. No. 6043 (Fig. 12).

Locality: Heuningnest Krantz, Graaff-Reinet.

This specimen consists of an occipital plate, the intertemporal region of the skull roof, the left jaw ramus and the symphyseal region of the fused dentaries.

The nature of the preserved dentary indicates that this dicynodont differed from all the specimens described above in the nature of the external adductor muscle insertion. There is a very deeply excavated dentary fossa, leading out laterally to a wide dentary shelf. There is no groove on the dorsal border of the dentary, which is reduced to a sharp edge above the lateral dentary shelf. Anterior to this region the dentary is rounded dorsally.

It appears that in this dicynodont, which in some respects resembles *Kingoria* (Cox, 1959), the insertion areas of both the external and internal adductor muscle masses were coalesced in the deep and wide dentary shelf.

DISCUSSION

Boonstra (1963) has outlined the main steps involved in the derivation of a typical dicynodont from a sphenacodont pelycosaur. The two Russian forms *Venjukovia* and *Otsheria* appear to be transitional in this evolutionary sequence. The main changes which took place in the palate are connected with the development of a premaxillary secondary palate and the reduction in the number of teeth.

The increase in palatal extent of the premaxilla, already far advanced in *Venjukovia* and *Otsheria*, results in the posterior displacement of the internal nares, and an associated dorsal vaulting of the palate posterior to the premaxilla. Thus in *Venjukovia* only a lateral portion of the palatine retains its original palatal disposition, the median section being strongly arched to form a posterodorsal roof for the emerging air passage. The maxilla assists in the posterior displacement of the functional choana by developing a median extension, which in some dicynodonts separates the premaxilla from the palatine. The ventral surface of the vomer, flush with the surrounding palatal bones in pelycosaurs, has been affected by the dorsal arching of the palatines, and in typical dicynodonts lies recessed in the palatal vault. In typical dicynodonts teeth anterior to the canine tusks have been lost, and postcanine teeth, where present, have migrated medially. A true alveolar border is absent.

The relationships between premaxilla, maxilla and palatine would by this analysis depend on the rate of posterior extension of the premaxilla, the degree of medial extension of the maxilla, and the degree of dorsal arching of the palatine. A further determining factor would be the shortening of the palatal region as a whole, a process which seems to have been active during the evolution of true dicynodonts from pelycosaur ancestors. Associated with these changes in the anterior portion of the skull, was the differentiation of the external adductor muscle into lateral and medial portions, the former division gaining an area of origin, unique among therapsids, below and lateral to the base of the zygomatic arch.

It is therefore not surprising that a variety of palatal types were evolved during the early phases of dicynodont evolution. The most obvious variation is the presence or absence of a palatine-premaxilla contact. Thus in two apparently closely related endothiodontid genera, *Emydops* and *Pristerodon*, a palatine-premaxilla contact is present in the former but absent in the latter. In the lower jaw of these genera, however, the dentaries appear to be basically similar, with dorsal dentary grooves and lateral dentary ledges.

Oudenodon resembles *Dicynodon* in the absence of post-canine teeth and the similar dorsal grooves and flat lateral surface of the dentaries. In both genera it seems that the dentaries have been deepened behind the symphysis to form dentary tables. However, in *Dicynodon* a palatine-premaxilla contact is consistently lacking, this contact being a feature of *Oudenodon*.

Dicynodon testudirostris resembles other species of *Dicynodon* in the presence of the median palatal process of the maxilla between the premaxilla and palatine. Departures from the typical dicynodontid condition are the reduced or absent canine tusks, the transformed and enlarged caniniform processes, the greatly reduced palatal portion of the palatine, the widely excavated dentary tables of the lower jaw and the rounded dorsal edge of the dentary.

It seems that these characteristics of *Dicynodon testudirostris* are specialisations leading away from the typical *Dicynodon* stock, rather than primitive features retained from an ancestral dicynodont group. The reduction of the

typical *Dicynodon* canine teeth and concomitant enlargement of the caniniform process was of adaptive value, connected with a reorganisation of the food cutting and crushing areas on the palate and buccal surface of the lower jaw. The anterior edge of the caniniform process appears to have taken over the slicing function of the more anterior palatal rim, which has no close association with the sides of the dentary during the masticatory cycle. Similarly, while in most typical dicynodonts the main food-crushing area in the palate is the expanded palatal portion of the palatine and a part of the adjoining maxilla, in *Dicynodon testudirostris* the food-crushing activity has been moved forward to the raised premaxillary-maxillary shelf median to the caniniform process. The palatine has been reduced accordingly.

In the symphyseal region of the lower jaw, the dorsal edge of the dentary, which in *Dicynodon* and *Daptocephalus* appears to have borne a simple thickening of horn, has become excavated to form a deep trough, which would have contained a greatly enlarged pad of the horny beak to work up against the raised maxillary-premaxillary shelf in the palate. Medially the trough is terminated as a high, sharp blade, which, produced in horn, would have acted as a sharp knife-edge in the trough alongside the median palatal ridge.

Associated with these changes was a new insertion of the medial division of the external adductor muscle. The sulcus in the dorsal edge of the dentary appears to have housed this insertion in forms which have retained post-canine teeth, such as *Emydops* and *Pristerodon*, as well as more advanced genera such as *Dicynodon*, *Lystrosaurus* and *Kannemeyeria*. There is a possibility that the insertion of this muscle mass in *Dicynodon testudirostris* migrated outwards onto the lateral surface of the dentary. That there was considerable variation in this part of the dentary among the various dicynodont groups has been shown, an extreme condition being the dentary of the dicynodont, S.A.M. Cat. No. 6043 (*Kingoria* ? sp.), where a coalescence of the insertions of the inner and outer division of the adductor muscle appears to have occurred in the wide and deeply moulded dentary ledge.

The features in the skull and mandible of *Dicynodon testudirostris* which represent a departure from the typical *Dicynodon* cranial pattern are adaptive modifications, clearly related to an attempt at achieving more effective mastication. *Dicynodon testudirostris* is in these respects clearly distinguishable from other species of *Dicynodon*, and the results of further investigation into the morphology of the genus *Dicynodon* itself may later warrant the inclusion of the species *testudirostris* in a different but related genus.

Summary

Several specimens of the therapsid *Dicynodon testudirostris* have been described, with special reference to the palate, palatal rim and mandible. The function of the unusual caniniform flange of the maxilla, and the occlusal relationships between upper and lower jaws during the masticatory cycle,

have been discussed. Comparison of *Dicynodon testudirostris* with other dicynodont genera has provided some indication of the steps involved in the evolution of the various main dicynodont groups.

Acknowledgements

Mrs. I. M. Chesselet and Miss S. A. James have, by their meticulous and painstaking preparation of the majority of the specimens, made an invaluable contribution to this project.

The Trustees of the South African Museum thank the South African Council for Scientific and Industrial Research for a grant in aid of publication.

References

Agnew, J. D. 1959. Cranio-osteological studies in *Dicynodon grimbeeki* with special reference to the sphenethmoid region and cranial kinesis. *Palaeont. afr.* **6**: 77–107.

Barry, T. H. 1967. The cranial morphology of the Permo-Triassic anomodont *Pristerodon buffaloensis* with special reference to the neural endocranium and visceral arch skeleton. *Ann. S. Afr. Mus.* **50**: 131–161.

Boonstra, L. D. 1963. Early dichotomies in the therapsids. *S. Afr. J. Sci.* **59**: 176–195.

Broom, R. 1932. *The mammal-like reptiles of South Africa and the origin of mammals.* London: Witherby.

Broom, R. & Haughton, S. H. 1913. On two new species of *Dicynodon*. *Ann. S. Afr. Mus.* **12**: 36–37.

Camp, C. L. & Welles, S. P. 1956. Triassic dicynodont reptiles. Part I. The North American genus *Placerias*. *Mem. Univ. Calif.* **13**: 255–304.

Cluver, M. A. (In press.) The cranial anatomy of the genus *Lystrosaurus*. *Ann. S. Afr. Mus.*

Cox, C. B. 1959. On the anatomy of a new dicynodont genus with evidence of the position of the tympanum. *Proc. zool. Soc. Lond.* **132**: 231–367.

Crompton, A. W. & Hotton, N. 1967. Functional morphology of the masticatory apparatus of two dicynodonts (Reptilia, Therapsida). *Postilla* **109**: 1–51.

Ewer, R. F. 1961. The anatomy of the anomodont *Daptocephalus leoniceps* (Owen). *Proc. zool. Soc. Lond.* **136**: 375–402.

Haughton, S. H. & Brink, A. S. 1954. A bibliographical list of Reptilia from the Karroo beds of Africa. *Palaeont. afr.* **2**: 1–187.

Romer, A. S. 1966. *Vertebrate paleontology*. 3rd ed. Chicago: University Press.

Toerien, M. J. 1953. The evolution of the palate in South African Anomodontia and its classificatory significance. *Palaeont. afr.* **1**: 49–117.

Abbreviations

ang.	angular	pal.	palatine
ant. pm. r.	anterior premaxillary ridge	pal. sh.	palatal shelf
art.	articular	pas.	parasphenoid
bas.	basisphenoid	pfr.	prefrontal
bo.	basioccipital	pil. ant.	pila antotica
can. fl.	caniniform flange	pm.	premaxilla
den.	dentary	po.	postorbital
den. fos.	dentary fossa	pof.	postfrontal
den. gr.	dentary groove	pp.	preparietal
den. l.	dentary ledge	prs.	presphenoid
den. r.	dentary ridge	pt.	pterygoid
ect.	ectopterygoid	q.	quadrate
eo.	exoccipital	qj.	quadratojugal
ept.	epipterygoid	ref. lam.	reflected lamina
fr.	frontal	sa.	surangular
ipt. vac.	interpterygoidal vacuity	smx.	septomaxilla
jug.	jugal	smx. for.	septomaxillary foramen
lac.	lacrimal	sq.	squamosal
lat. den. sh.	lateral dentary shelf	sta.	stapes
max.	maxilla	t.	tooth
med. pm. r.	median premaxillary ridge	tub.	tubercle
nas.	nasal	vo.	vomer
orb.	orbitosphenoid	VII	foramen for facial nerve
pa.	parietal	XII	foramen for hypoglossal nerve

INSTRUCTIONS TO AUTHORS

Based on

CONFERENCE OF BIOLOGICAL EDITORS, COMMITTEE ON FORM AND STYLE. 1960.

Style manual for biological journals. Washington: American Institute of Biological Sciences.

MANUSCRIPT

To be typewritten, double spaced, with good margins, arranged in the following order: (1) Heading, consisting of informative but brief title, name(s) of author(s), address(es) of author(s), number of illustrations (plates, figures, enumerated maps and tables) in the article. (2) Contents. (3) The main text, divided into principal divisions with major headings; subheadings to be used sparingly and enumeration of headings to be avoided. (4) Summary. (5) Acknowledgements. (6) References, as below. (7) Key to lettering of figure. (8) Explanation to plates.

ILLUSTRATIONS

To be reducible to 12 cm × 18 cm (19 cm including caption). A metric scale to appear with all photographs.

REFERENCES

Harvard system (name and year) to be used: author's name and year of publication given in text; full references at the end of the article, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year.

For books give title in italics, edition, volume number, place of publication, publisher.

For journal articles give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*. 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination.

Examples (note capitalization and punctuation)

BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.

FISCHER, P.-H. 1948. Données sur la résistance et de le vitalité des mollusques. *J. Conch., Paris* **88**: 100–140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* **74**: 627–634.

KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) **2**: 309–320.

KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* **17** (4): 1–51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. *In* SCHULTZE. L, *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika*. **4**: 269–270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* **16**: 269–270.

ZOOLOGICAL NOMENCLATURE

To be governed by the rulings of the latest *International code of zoological nomenclature* issued by the International Trust for Zoological Nomenclature (particularly articles 22 and 51). The Harvard system of reference to be used in the synonymy lists, with the full references incorporated in the list at the end of the article, and not given in contracted form in the synonymy list.

Example

Scalaria coronata Lamarck, 1816: pl. 451, figs 5 *a*, *b*; Liste: 11. Turton, 1932: 80.